

Inflorescence and flower development in *Costus scaber* (Costaceae)

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Abstract:

The inflorescence of *Costus scaber* terminates an erect axis of a sympodial rhizome system. Primary bracts are borne on the inflorescence in spiral monostichous phyllotaxy. One-flowered cincinni occur in the axils of these bracts. Each cincinnus consists of an axis bearing a terminal flower and a secondary bract on the anodic side of the flower. A tertiary bud forms in the axil of this bract but does not complete development. The inflorescence terminates by cessation of growth of the apex and precocious development of the primary bracts. Floral organs are formed sequentially beginning with the calyx, and continuing with the corolla and inner androecial whorl, outer androecial whorl, and gynoecium. All flower parts, except for the calyx, originate from a ring primordium. Regions of this primordium separate to form the corolla and inner androecial members. It was not possible to determine the sequence of androecial member formation. The labellum is composed of five androecial members, three from the outer whorl and two from the inner. The third member of the inner whorl forms the stamen and its petaloid appendage. The gynoecium forms from three conduplicate primordia. The margins of two of these primordia are the product of phyletic fusion.

L'inflorescence du *Costus scaber* termine un axe dressé d'un système de rhizome sympodique. Les bractées primaires sont portées sur [inflorescence selon une phyllotaxie spirale monostique. Des cincinnus unilobes sont présents dans l'aisselle de ces bractées. Chaque cincinnus est constitué d'un axe portant une fleur terminale et une bractée secondaire sur le côté anodique de la fleur. Un bourgeon tertiaire naît dans l'aisselle de cette bractée mais ne se développe pas complètement. L'inflorescence termine par un arrêt de la croissance de l'apex et le développement précoce des bractées primaires. Les organes floraux sont formés de façon séquentielle, débutant avec le calice et continuant, dans l'ordre, avec la corolle et le verticille staminal interne, le verticille staminal externe et le gynécée. Toutes les pièces florales, à l'exception du calice, naissent d'un primordium annulaire. Des régions de ce primordium se distinguent pour former la corolle et les pièces internes de l'androcée. Il n'a pas été possible de déterminer la séquence de formation des membres de l'androcée. Le labelle est formé de cinq membres de l'androcée, trois du verticille externe et deux du verticille interne. Le troisième membre du verticille interne forme l'étamine et son appendice pétaloïde. Le gynécée provient de trois primordiums condupliqués. Les marges de deux de ces primordiums montrent une fusion congénitale.

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Article:

INTRODUCTION

The Costaceae are a monocotyledonous family of plants closely related to the Zingiberaceae. Both families belong to the order Zingiberales. *Costus*, with its allied genera *Monocostus* and *Dimerocostus*, may be separated from the Zingiberaceae on the basis of several characters. The Costaceae are characterized by spiral monostichous phyllotaxy, closed leaf sheaths, druse-like silica bodies, a stem demarcated into a cortex and central cylinder by a fluted fibrous cylinder, and the lack of aromatic compounds. The Zingiberaceae are characterized by distichous phyllotaxy, open leaf sheaths, spherical silica bodies, a stem demarcated into a cortex and central cylinder by a smooth fibrous cylinder, and the possession of aromatic compounds (Schumann 1904; Panchaksharappa 1962; Tomlinson 1962). Inflorescence structure also differs between these families. As part of a study of the inflorescences of the Zingiberales (Kirchoff 1986) this paper presents the structure and development of the inflorescence and flowers of *Costus scaber* Ruiz et Pavon.

MATERIALS AND METHODS

Living material of *Costus scaber* was collected at Fairchild Tropical Garden, Miami, FL, U.S.A. (FTG accession number P.609). A voucher is deposited at FTG (Kirchoff 84-6). Vegetative and inflorescence apices, along with floral apices, were fixed in formalin — acetic acid — alcohol (FAA: 50 mL 95% ethanol, 5 mL glacial acetic acid, 10 mL 40% formalin, 35 mL H₂O). An epillumination, light microscopy technique (Sattler 1968; Posluszny et al. 1980) was used in this study.

Fixed material was dehydrated to 100% ethanol and stained for 1 week in Johansen's fast green (Johansen 1940). Destaining was carried out in 100% ethanol for 2-7 days. Photographs were taken with Kodak Technical Pan film on a Leitz Ortholux 2 photomicroscope equipped with an Ultropack illuminator. Kodak Technical Pan film was found to give the best results when developed for 3 min in Dektol at 20°C. After photography, the buds were transferred to tert-butyl alcohol and embedded in "Tissue-prep," a paraffin embedding medium. Sections were cut at 5 µm on an American Optical 820 microtome. The sections were stained in tannic acid — ferric chloride, safranin, and fast green (Berlyn and Miksche 1976) and mounted in "Kleermount." Measurements of apical dome size were made from sectioned material, using an ocular micrometer on a Leitz Ortholux 2 microscope. Because of scarcity of suitable material and difficulty in sectioning, only one bud was measured at each stage.

RESULTS

Organographv

Costus scaber is a rhizomatous plant with sympodial growth. Each shoot arises in the axil of a cataphyll, grows horizontally for a short distance, and turns up to produce an erect axis. A renewal shoot arises in the axil of a cataphyll at the base of the erect axis. An inflorescence generally terminates each axis (Fig. 1), although some apices abort during inflorescence production.

Each axis of the sympodium produces between 11 and 19 cataphylls and from 18 to 42 foliage leaves. The number of foliage leaves produced seems to be related to the amount of time

between a shoot's emergence and when it flowers. The inflorescence produces between 50 and 82 bracts over a period



FIG. 1. Inflorescence of *Costus scaber* terminating a leafy shoot. x0.67.

of several months. At Fairchild Tropical Garden the period of floral anthesis extends from April to September, although no single inflorescence produces flowers over this entire period.

The divergence angle between successive phyllomes is unusually small in the Costaceae, giving rise to the spiral monostichous phyllotaxy that characterizes the family (Von Veh 1931; Smith 1941; Snow 1952). In the inflorescence the divergence angle increases from 45-55°, typical of the upper vegetative regions, to 50.76°, typical of the middle of the inflorescence. In the distal regions of the inflorescence the divergence angle increases again to 70-92°.

Each primary bract on the main inflorescence axis bears a nectary on its abaxial surface (Maas 1972; Elias 1983) and subtends a one-flowered cincinnus. Each cincinnus consists of an axis bearing a terminal flower and a single, secondary bract (Fig. 2, sb). A bud arises in the axil of this bract but ceases development at an early stage of growth. Within an inflorescence all cincinni are of the same handedness. The handedness of the cincinni varies between inflorescences.

The lateral regions of each flower can be designated anodic and cathodic. The anodic side is the side in the direction of the rise of the phyllotactic helix (Fig. 2, an), while the cathodic is the side opposite the direction of the rise of the phyllotactic helix (Fig. 2, ca). The secondary bract is always on the anodic side of the flower (Eichler 1884).

Each flower (Fig. 2) consists of a gamosepalous calyx that is shallowly three lobed, a floral tube uniting the corolla and androecium, and a trilobulate inferior ovary with many ovules per locule. The corolla is divided into three free segments above the floral tube. The androecium is composed of a labellum and a functional stamen. The stamen consists of two locules positioned side by side on the ventral surface of a petaloid appendage. The style is held between the thecae, with the stigma positioned near the top of the anther. Nectar glands situated at the top of the ovary secrete nectar into the floral tube (Rao 1963).

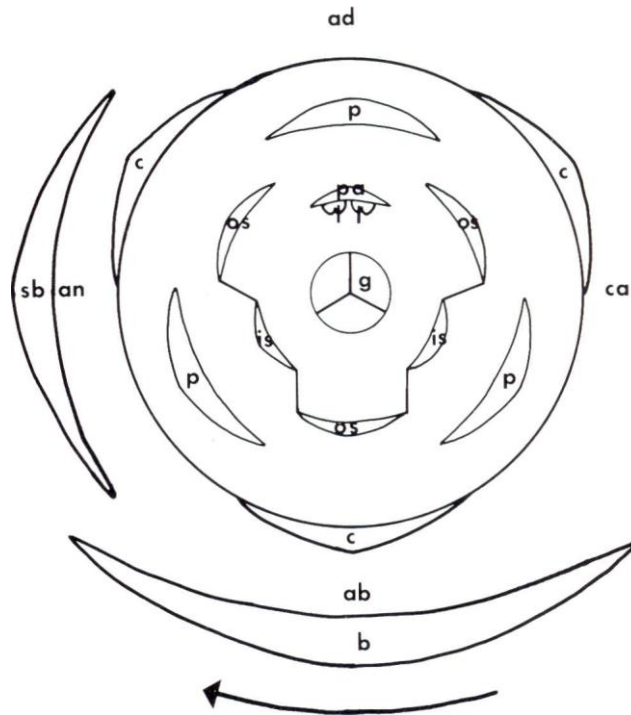


FIG. 2. Diagram of cincinnus and flower structure in *Costus scaber*. The labellum is shown composed of five staminodes, three from the outer androecial whorl (*os*) and two from the inner androecial whorl (*is*). The abaxial (*ab*), adaxial (*ad*), anodic (*an*), and cathodic (*ca*) directions are indicated. Abaxial and adaxial are determined with respect to the inflorescence axis. Anodic and cathodic are determined with respect to the direction of phyllotaxy (arrow). *b*, primary bract; *c*, sepal; *g*, gynoecium; 1, locules of stamen; *p*, petal; *pa*, petaloid appendage of stamen; *sb*, secondary bract. All additional polar views are oriented in the same way as this diagram.

Vegetative apex

A vegetative apex actively producing foliage leaves is a domed more or less symmetrical apex (Fig. 3) with a free apical dome approximately 49 high and 150 Am wide. By the third or fourth plastochron after initiation, the margins of the primordium surround the axis and produce the leaf sheath. At this stage, the distal portion of the primordium covers the apex from above (Fig. 3).

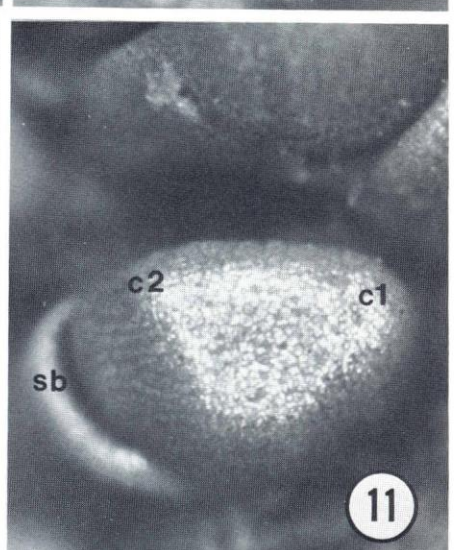
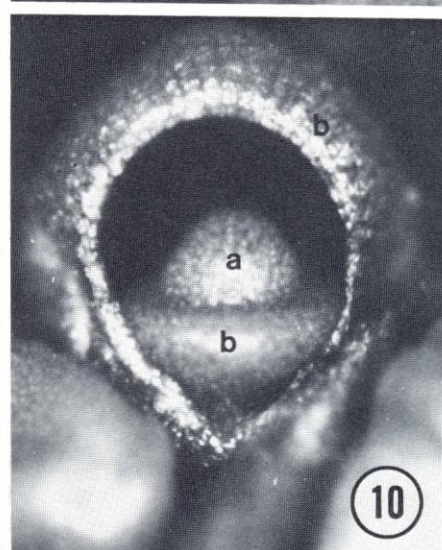
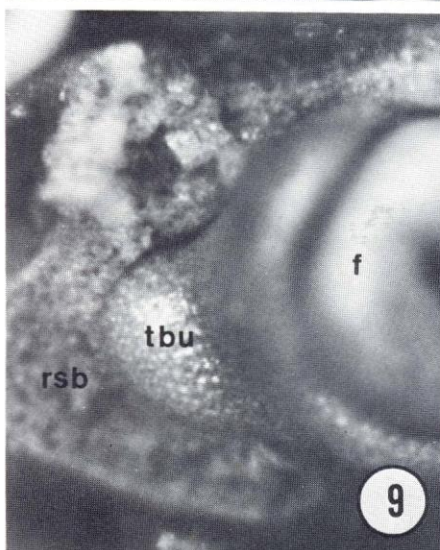
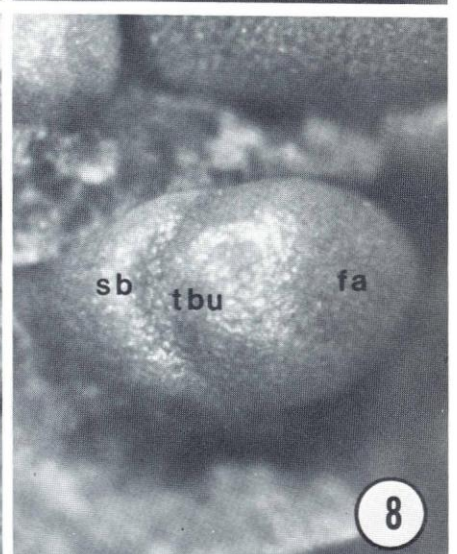
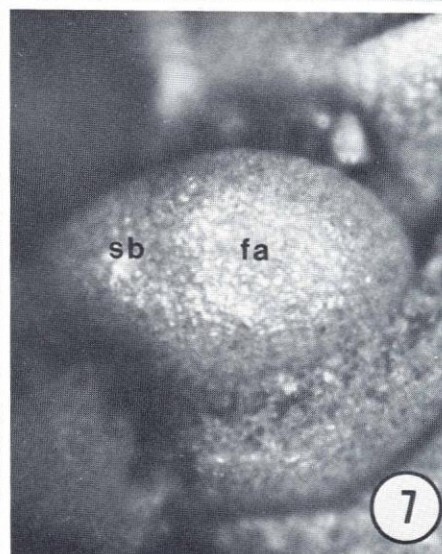
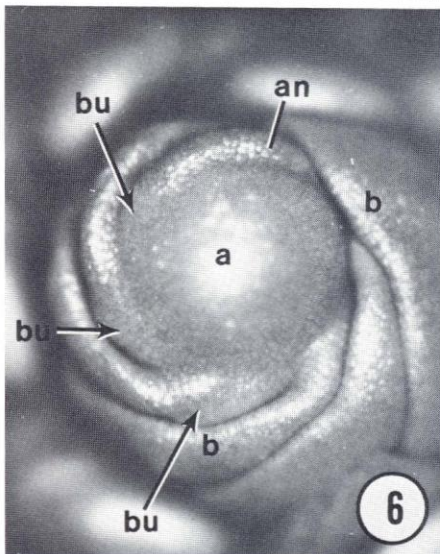
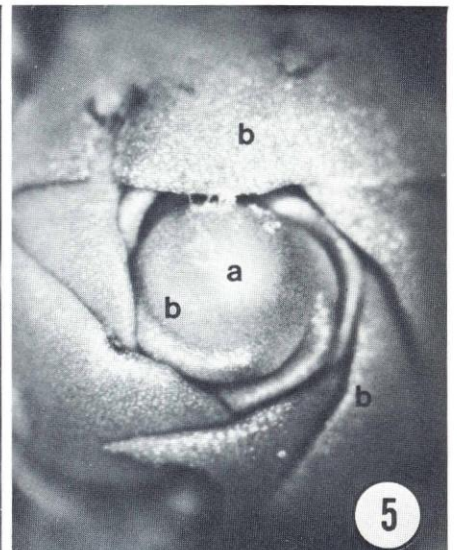
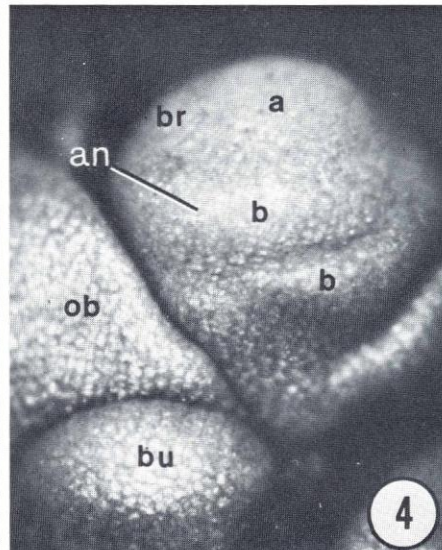
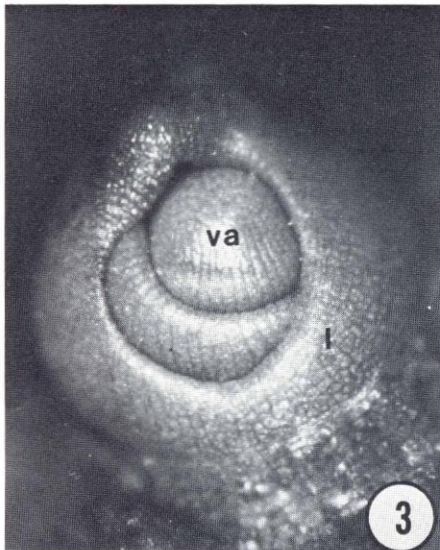
Inflorescence development

The inflorescence apex is shallowly domed and produces bracts on the side of the dome (Fig. 4). The free apical dome has a height of approximately 27 pun and a width of approximately 140 Am. The inflorescence apex appears larger than the vegetative apex because the youngest bracts do not enlarge as early or as rapidly as the vegetative leaves.

The inflorescence apex is tilted in the direction in which the next bract will appear (Fig. 5). This asymmetry may result

FIG. 3. Vegetative apex (*va*) and leaves (*l*). x94.9. FIG. 4. Inflorescence apex (*a*) and primary bracts (*b*, *br*, *ob*) from the side. *an*, anodic portion of primary bract (P_2); *br*, most recently formed primary bract; *bu*, bud in axil of primary bract; *ob*, older primary bract. x 132. FIG. 5. Inflorescence apex (*a*) and primary bracts (*b*) from above. Note that the bracts do not cover the apex until several plastochrons after initiation. x67.5. FIG. 6. Inflorescence apex (*a*) showing separation of primary bracts (*b*) from the apex, and formation of axillary buds (*bu*). *an*, anodic portion of primary bract. x64.6. FIG. 7. Flower apex (*fa*) and recently separated secondary

bract (*sb*). x 156. FIG. 8. Oblique view of flower apex (*fa*) showing formation of third-order bud (*tbu*). *sb*, secondary bract. x 142.6. FIG. 9. Aborted third-order bud (*tbu*) in the axil of a (removed) secondary bract (*rsb*). *f*, flower bud. x 164. FIG. 10. Aborted inflorescence apex (*a*). Note that the primary bracts (*b*) expand to cover the apex after only two or three plastochrons. x 153.2. FIG. 11. Flower primordium showing formation of the adaxial cathodic sepal (*c*/, first- formed sepal) and adaxial anodic sepal (*c*2, second-formed sepal). *sb*, secondary bract. x 136.8.



from an early widening of the apex in preparation for bract formation, or from an actual inclination of the apex. It was not possible to distinguish between these two hypotheses in this study.

Unlike foliage leaves, the bracts do not completely surround the inflorescence axis (Fig. 4), nor do they cover the apex within several plastochrons of initiation (Fig. 5). Only after more than 11 plastochrons does a bract begin to cover the apex.

Bracts are first seen in surface view as small protrusions on the side of the apical dome (Fig. 4, br). Bract formation occurs unevenly along the lateral extent of the bract. The anodic portion of the bract is formed slightly lower on the apex than is the cathodic (Figs. 4, 6, an). The young bracts appear in a tightly overlapping spiral when viewed from above (Figs. 5, 6).

A bud is formed in the axil of the bract in approximately the third plastochron of growth (P3). The bud arises very close to the cathodic margin of the next younger (P2) bract primordium (Fig. 6). Continued differentiation of the younger bract (P2) in the cathodic direction (Fig. 6) positions the bud on the abaxial side of the bract (P2) (Fig. 4, ob, ha).

Cincinnus development

After initiation, the bud in the axil of the primary bract enlarges to produce a tangentially extended primordium, relative to the inflorescence axis (Fig. 4, bu). The first sign of secondary bract (SB) formation is a slight inequality in the shapes of the anodic and cathodic portions of the primordium. A triangular primordium then separates from the anodic side of the bud to form the SB (Fig. 7, sb). Separation of the SB leaves the anodic side of the flower apex distinctly flattened (Fig. 7). A third-order bud forms from this flattened region, in the axil of the SB (Fig. 8, tbu). After a short period of enlargement, this bud aborts (Fig. 9, tbu). No higher order bracts or buds are formed in the cincinnus.

Termination of the inflorescence

The inflorescence terminates through the cessation of growth of the apex (Fig. 10). Several sterile bracts may be produced before the cells of the apex vacuolate and cease division. Bract expansion occurs closer to the apex as the inflorescence terminates, so that by the second or third plastochron a bract has already covered the apex. In this process, a cavity is created around the apex (Fig. 10). The free apical dome of a terminating apex is approximately 58 pcm high and approximately 111 Am wide.

Flower development

Preceding and during secondary bract formation the bud in the axil of the primary bract continues to enlarge. Radial expansion of the bud produces a flattened primordium (compare Figs. 4, bu; 7 and 8). At the stage of SB formation the remaining portion of the bud, which will form the flower, has a rounded triangular appearance (Fig. 7, fa). The center of the flower primordium is slightly depressed with respect to the surrounding tissue. This inequality of development is a very early stage in the formation of the ring primordium (RP). The RP will give rise to all of the flower parts, except the calyx. A slightly later stage in the formation of the RP is visible at the stage of sepal formation (Fig. 11).

Floral organ formation is sequential, not generally simultaneous. However, in certain apices two or more organs may appear simultaneously. The general sequence of organ formation between whorls is calyx, corolla and inner androecial whorl, outer androecial whorl, gynoecium. The exact sequence of development within the corolla and androecial whorls (and occasionally between whorls) is unclear as a result of interbud variability.

Sepal formation begins concurrently with, or slightly later than, formation of the bud in the axil of the SB. The first sepal is always formed opposite the SB on the adaxial cathodic side of the apex (Fig. 11, c/). The second sepal is formed on the adaxial anodic side of the apex, more or less opposite the cathodic sepal (Fig. 11, c2). At this stage of development the floral apex is slightly larger adaxially than abaxially and has a trapezoidal appearance in surface view. As sepal formation proceeds, the RP continues to develop and becomes more distinctly circular (Fig. 12, rp). Formation of the third, abaxial, sepal is delayed with respect to the first two. It is formed only after the RP is well developed (Fig. 12, c3). Intercalary growth between the sepals produces the gamosepalous calyx (Fig. 14). The RP gives rise to all of the remaining floral parts.

The three petals and their associated inner androecial members are formed through the separation of three portions of the RP. Each of these portions separates into a dorsal petal and a ventral androecial member. The term common primordium (CP) will be used to designate a region of the RP that produces two floral members. However, the RP is a continuous structure. The CPs have only been designated to facilitate communication. In *Costus scaber* there are three CPs that produce the corolla and inner androecial members.

Differentiation of the petals from their associated androecial members is slightly different in the CPs producing the staminodes and the CP producing the functional stamen. The stamen is formed in the adaxial region of the RP. This region widens to produce a slightly flattened CP (Fig. 13, cp), then divides into the petal and stamen (Fig. 14, p, s). Separation of the petal and stamen is evident with the appearance of a depression in the center of the CP (Fig. 14). Division of the lateral portions of the CP does not take place until the stage of outer androecial formation (Fig. 15, unlabeled arrows).

Growth of the anodic and cathodic abaxial portions of the RP produces petals (dorsally) and inner staminodes (ventrally). The CPs first enlarge dorsally and ventrally to produce flattened primordia (Fig. 14, cp). Division of the CPs is completed by growth of the dorsal and ventral regions to produce discrete primordia (Fig. 15, is, p). It has proven impossible to determine the sequence of inner androecial formation. While some buds appear to show a spiral sequence of formation, others appear to show simultaneous formation of the androecial members.

Outer androecial formation takes place on the portions of the RP left vacant by the formation of the corolla and inner androecium. As the CPs separate, three portions of the RP become visible as separate outer androecial primordia (Fig. 15, os). This is the first sign of the presence of the outer androecial whorl. Further growth produces more distinct primordia in these regions (Fig. 16, os). The outer androecial members remain attached to those of the inner whorl throughout development.

The sequence of appearance of the outer staminodes is difficult to determine. However, one staminode usually appears larger than the others (Fig. 15, os and arrow), so their formation is not simultaneous.

The adaxial anodic and cathodic outer staminodes appear as distinct primordia when they swell outward away from the center of the flower (Fig. 16, os without arrow). The abaxial

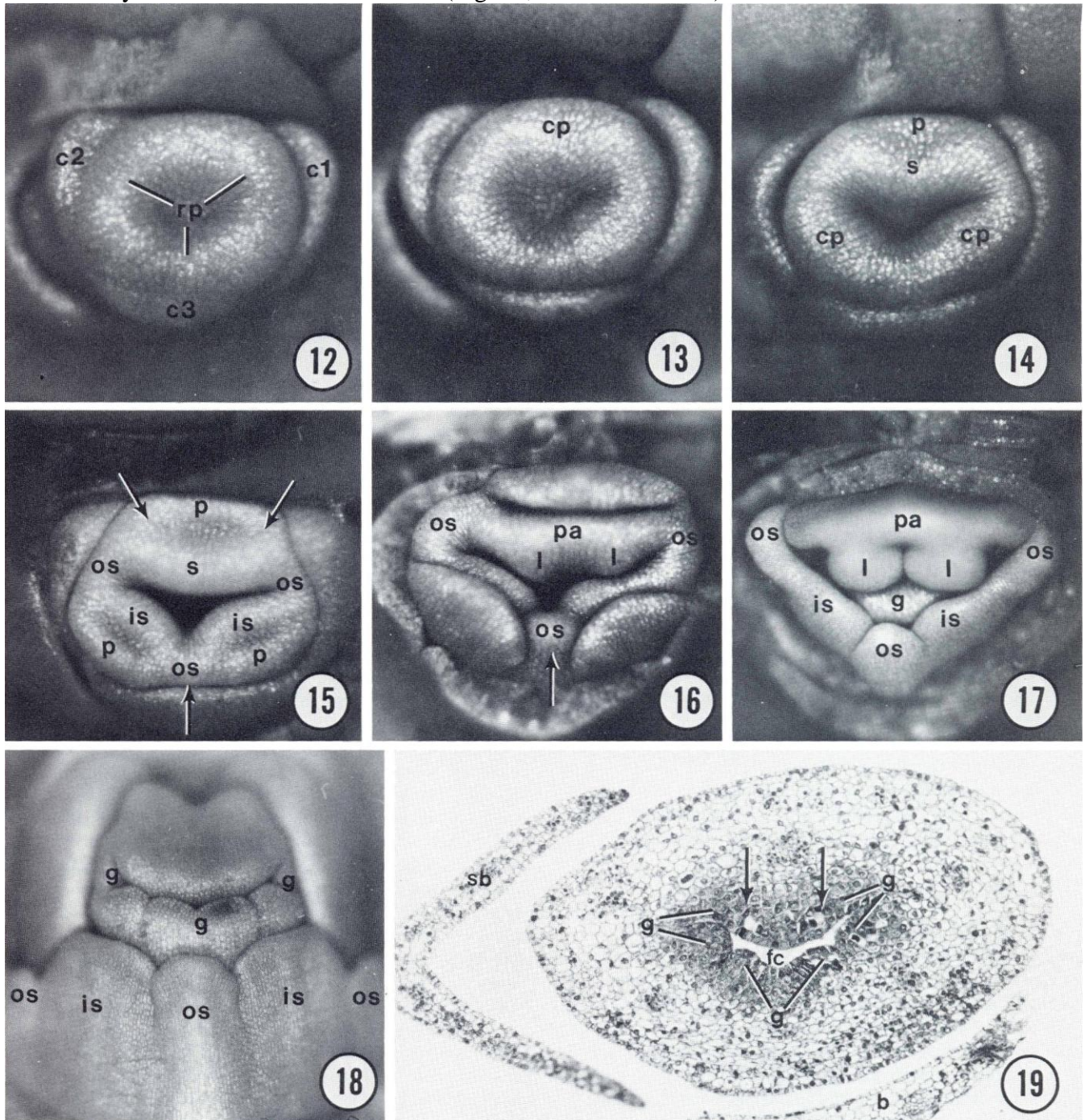


FIG. 12. Flower primordium with a well-developed ring primordium (*rp*) and three sepals (*cl* — *c3*). x 136. FIG. 13. Flower primordium showing widening of adaxial common primordium (*cp*). x 127.5. FIG. 14. Flower primordium showing flattened common primordia (*cp*) and separation of the stamen (*s*) and petal (*p*) in the adaxial region. x 121.6. FIG. 15. Flower primordium at the stage of outer androecial formation. Unlabeled arrows, lateral portions of the petal — stamen CP just beginning to separate; *is*, inner staminode; *os*, outer staminode; *os* and arrow, first-formed outer staminode (abaxial outer staminode); *p*, petal; *s*, stamen. x 106.2. FIG. 16. Flower primordium showing differentiation of the outer androecial whorl (*os*), and locule formation (l) in the stamen. The sepals have been removed. Arrow, first-formed outer staminode (abaxial outer staminode); *pa*, petaloid appendage of the stamen. x 100.2. FIG. 17. Flower bud after formation of all floral parts. The sepals and petals are removed. The labellum is composed of the inner (*is*) and outer (*os*) staminodes. *g*, gynoecium; l, locule of anther; *pa*, petaloid appendage of stamen. x 78.3. FIG. 18. Flower bud showing labellum composed of five androecial members (*is*, *os*), and stigma composed of three gynoecial members (*g*). The calyx and corolla have been removed. *is*, inner staminode; *os*, outer staminode. x 61.9. FIG. 19. Cross section through an ovary at the time of gynoecial formation. The three gynoecial primordia are formed on the ventral margins of the floral cup (*fc*). Arrows, congenitally fused margins of adjacent conduplicate primordia; *b*, primary bract; *sb*, secondary bract. x 132.5.

staminode becomes distinct through lateral separation from the adjoining members of the inner whorl (Fig. 16, arrow). At an early stage of growth this staminode appears as an oval bulge, while the adaxial staminodes appear crescent shaped (Fig. 16).

All five staminodial androecial members remain united after formation and produce the labellum (Figs. 2, 17, 18 (The labellum is composed of the five androecial members labeled *is* and *os*)). Thus, the labellum is composed of two inner and three outer androecial members. Only the apical portions of the staminodes remain free. They contribute to the fringe of the mature labellum.

After the formation of the inner and outer androecial whorls, two bulges appear on the ventral surface of the stamen primordium (Fig. 16, l). These bulges grow radially into the center of the flower and give rise to the locules of the anther (Fig. 17, l). The dorsal portion of the stamen primordium gives rise to the petaloid appendage of the anther (Figs. 16, 17, *pa*). The formation of the anther and the petaloid appendage are simultaneous. As growth continues, the stamen becomes separated from the labellum (Figs. 2, 17).

Intercalary growth of the RP before and during organogenesis produces a floral cup in the center of the flower (Figs. 15; 19.10). The ventral margins of this cup produce the gynoecial primordia (Fig. 19, *g*). Proximally, these primordia form the septa, distally, the stigma and style (Fig. 18, *g*).

Three primordia can be seen in a cross section of the ovary at the stage of gynoecial formation (Fig. 19, *g*). Each primordium is conduplicate. As growth continues, the margins of the primordia grow inward, fuse with the adjacent primordia (Fig. 19), and eventually enclose the locules (Fig. 20, lo). The margins of all three primordia contribute to the collum of tissue in the center of the ovary (Fig. 20, ax). The margins of two of the conduplicate primordia (Fig. 19, arrows) are joined by phyletic fusion (Sattler 1978) to form a single bulge in the adaxial portion of the young ovary.

Although the origin of the floral nectaries was not investigated in detail, the external portions of the nectaries result from outgrowths of the gynoecial primordia, above the ovary.

DISCUSSION

The inflorescence of *Costus scaber* consists of an axis bearing one-flowered cincinni in the axils of bracts. It terminates by cessation of growth of the apex. It may thus be designated a polytelic synflorescence following the terminology of Troll (1964) and Weberling (1965). In this classification each cymose lateral branch is termed a partial florescence. Although only one flower of each partial florescence develops in this species, an abortive bud is formed in the axil of each secondary bract. No higher order bracts or buds are formed.

The placement of bracts on the inflorescence axis is unusual for two reasons. First, the divergence angle between bracts is very low. At the base of the inflorescence it can be as low as 50°. Second, bract development is not symmetrical at the apex. The anodic portion of the bract arises slightly lower on the apex than the cathodic. Von Veh (1931) noticed this in the mature inflorescence of *Costus*.

A number of terms have been applied to the phyllome that is here referred to as a secondary bract. In the taxonomic literature it is generally referred to as a bracteole (Schumann 1904; Maas 1972). However, this term is most correctly applied to phyllomes that develop from an apex that will produce only flower parts beyond the bracteole (S. Tucker and N. Uhl, per-

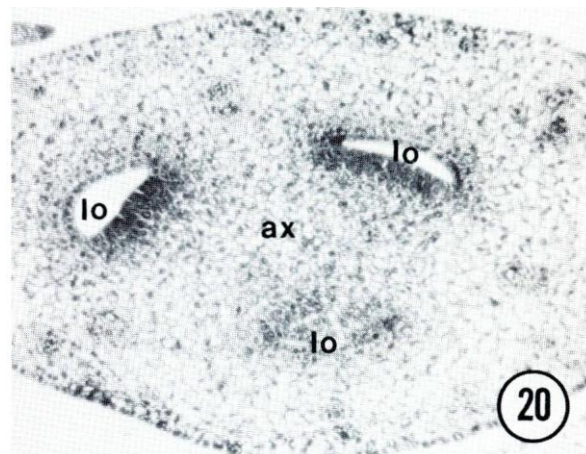


FIG. 20. Cross section through an ovary after formation of the locules (*lo*). *ax*, axial tissue of the ovary formed by the fusion of all three gynoecial primordia. x95.6.

sonal communication). The term seems to be misapplied here because a bud is produced in the axil of this phyllome. Since the phyllome in question is the first to appear on a lateral axis of the inflorescence, it is a prophyll (Schumann 1904). However, this term only serves to identify the phyllome as the first to occur on an axis. The term secondary bract was applied to this phyllome in the Zingiberaceae by Holttum (1950). This term serves to distinguish the phyllome from other prophylls occurring on higher order axes, where these occur, and from the primary bracts of the inflorescence. The term is appropriate because the bract is born on a second-order axis.

Placement of the secondary bract on the anodic side of the cincinnus is unusual. In the Zingiberaceae placement of the secondary bract is variable within an individual. In some cincinni it is anodic, in others cathodic (Eichler 1884: B. K. Kirchoff, personal observation). The placement of this bract on the anodic side in *Costus* means that all of the cincinni within an inflorescence have the same handedness. Between inflorescences with different directions of

bract phyllotaxy (sinistrorse or dextrorse) the cincinni are of opposite handedness, and are thus mirror images of each other. In inflorescences with sinistrorse phyllotaxy the secondary bract is on the left side of the cincinnus (as viewed from above), while in those with dextrorse phyllotaxy it is on the right.

The composition of the labellum in the Costaceae has long been debated. Costerus (1915) reviewed the literature on the composition of the labellum of the Zingiberaceae sensu lato (including Costaceae) to 1915, and concluded that it is five parted in *Costus*. Troll (1928) studied the shape of the labellum in *Costus* and concluded that it is composed of five staminodes, two belonging to the inner whorl and three to the outer whorl. Rao et al. (1954) were unable to reach any conclusions about the nature of the labellum based on vascular anatomy. The presence of a vascular plexus at the top of the ovary prevented them from tracing the origin of the bundles supplying the labellum.

The results presented in this paper clearly support the typological interpretation of the labellum as five parted. The two staminodial members of the inner androecial whorl are formed before the members of the outer androecial whorl. Intercalary growth below the free portions of all five primordia produces most of the labellum.

The development of the petaloid appendage of the stamen takes place at the same time as the formation of the anther. While the ventral portion of the stamen primordium produces two bulges to form the anther, the dorsal portion extends laterally and vertically to form the petaloid appendage. This pattern is different from that described by Leinfellner (1956) in the Zingiberaceae. He found that the petaloid appendage was formed late in development. For this reason he regarded it as an accessory structure. This conclusion is not supported by the development of *C. scaber*.

The description of the gynoecium as arising from three con- duplicate primordia is in accordance with the descriptions of gynoecial development in the Marantaceae and Cannaceae (Kirchoff 1983). The one unusual feature reported for *C. scaber* is the phyletic fusion of the margins of two of the primordia.

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